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MALE PARENTAL CARE IN GREATER RHEAS (*RHEA AMERICANA*) IN ARGENTINA

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ABSTRACT.—Greater Rheas (*Rhea americana*) are precocial birds that show uniparental male care. We evaluated the extent of nest attention by males and estimated its effect on viability and survival of eggs. We assessed whether male absences during incubation were constrained to avoid embryos reaching lethal temperatures or to minimize risk of egg predation. We estimated (1) effect of nest attention on viability of eggs by comparing egg temperature in nests with and without male attention; and (2) effect of male care on egg predation, by comparing survival of eggs in nests with and without male care. Rhea males attended the eggs for 42 days, but effective incubation started 5–7 days after laying of the first egg. The proportion of time that males spent at the nest increased from 64% during egg laying (days 1–10) up to 97.5% during mid and late incubation (days 20–40). Male absences occurred at the warmest hours of the day and their lengths were positively correlated with the temperature of the environment. Male nest attention reduced the rate of egg losses and kept eggs above lower lethal temperatures for embryos during the night. We also estimated relative cost of parental care after hatching by comparing the time allocated to feeding and vigilance by males with chicks, males in nonreproductive groups, and nonreproductive solitary males. Males took care of the chicks for 4–6 months. They allocated less time to feeding and more time to vigilance than males in groups of adults or solitary males. Investment in vigilance decreased as chicks aged. Our results indicate that Greater Rhea males would require high levels of energetic reserves to start a breeding attempt. That high demand could explain why less than only 20% of the males attempt to nest during a breeding season. *Received 24 October 2001, accepted 17 December 2002.*

RESUMEN.—Rhea americana es un ave precocial que presenta cuidado uniparental por parte del macho. Evaluamos el grado de atención de los machos sobre el nido y estimamos su efecto sobre la viabilidad y sobrevivencia de los huevos. También evaluamos si las ausencias del macho durante la incubación estuvieron restringidas para evitar que los embriones alcanzaran temperaturas letales o para minimizar el riesgo de depredación de los huevos. Para ello estimamos: (1) El efecto de la atención del nido sobre la viabilidad de los huevos, comparando la temperatura de éstos en nidos con y sin atención del macho; y (2) el efecto del cuidado del macho sobre la depredación de los huevos, comparando la sobrevivencia de éstos en nidos con y sin cuidado parental. Los machos de Rhea atendieron los huevos durante 42 días, pero la incubación efectiva comenzó 5–7 días después de la puesta del primer huevo. La proporción del tiempo que los machos permanecieron en el nido aumentó del 64% durante la puesta de huevos (días 1–10) al 97.5% durante la incubación avanzada (días 20–40). Las ausencias del macho ocurrieron durante las horas más cálidas del día y la longitud de las ausencias se correlacionó positivamente con la temperatura ambiental. La atención del nido por parte del macho redujo la tasa de pérdida de huevos y mantuvo la temperatura de los huevos por encima de los valores letales para los embriones durante la noche. También estimamos el costo relativo del cuidado parental luego de la eclosión de los polluelos, comparando el tiempo que machos con polluelos, machos en grupos no reproductivos y machos solitarios no reproductivos, dedicaron a la alimentación y vigilancia. Los machos cuidaron de los polluelos durante 4-6 meses y éstos dedicaron un menor tiempo a la alimentación y un mayor tiempo a la vigilancia que los machos en grupos de adultos o solitarios. La inversión en vigilancia disminuyó con la edad de los polluelos. Nuestros resultados indican que los machos de Rhea necesitarían grandes reservas energéticas para poder iniciar un intento reproductivo. Esa alta demanda energética podría explicar por qué menos del 20% de los machos intentan nidificar durante una estación reproductiva.

PARENTAL CARE IN birds involves investment of time and energy in activities such as building a nest; production, laying, and incubation of eggs; and feeding and defense of chicks (Clutton-Brock 1991). Parental care of eggs occurs in all bird species with the exception of brood parasites and megapodes. In contrast, the extent of parental care of chicks vary widely among birds

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with some species (altricial birds) feeding their chicks intensively and others (precocial birds) investing mainly in chick defense (Lack 1968). Relative parental expenditure of each sex also varies extensively among birds. In ~90% of species, both sexes share the care of the young, although females usually invest more than males (Lack 1968). In the majority of the remaining species, females perform most parental duties but in ~1% of the cases, males are responsible for the care of eggs and chicks (Lack 1968). All species with uniparental male care have precocial young and exhibit a wide variety of mating systems, from monogamy to a combination of polyandry and polygyny (Clutton-Brock 1991). Reasons for the evolution of uniparental male care are poorly understood and explanations vary between species (see Clutton-Brock 1991 for a review).

It is generally accepted that the placement, attendance, and defense of the nest are the main factors that determine the viability of eggs and the rate of nest predation (Arnold et al. 1987, Martin 1995, Cresswell 1997). Constancy during incubation provides a favorable thermal environment for the development of embryos and protects eggs from extreme temperatures that could affect their hatchability (Grant 1982). In species in which only one sex incubates, there is a trade-off between attendance and defense of the nest and maintenance of a favorable energy balance (Thompson and Ravelin 1987, Flint and Grand 1999). Thermal requirements of embryos may constrain the timing and length of the foraging trips during incubation (Webb 1987). In addition, nest attention can decrease the risk of egg predation either by active nest defense or as a result of a reduction of the incubation period of eggs, and therefore a reduction of time they are exposed to predators (Clutton-Brock 1991, Creswell 1997, Flint and Grand 1999).

In Greater Rheas (*Rhea americana*), parental care is performed exclusively by males, with females restricting their investment to the production and laying of eggs. Rhea males build the nest, incubate the eggs, and care for the chicks after hatching (Muñiz 1885, Bruning 1974, Fernández and Reboreda 1998). In that species, the mating system combines harem polygyny and sequential polyandry (Muñiz 1885, Bruning 1974). Early in the breeding season (August–September) males compete for, and defend a group or harem of five to seven females. The male copulates with the females at least once every two to three days. Females lay eggs every 48 h for 10–12 days in a communal nest (Bruning 1974, Fernández and Reboreda 1998). Chicks hatch synchronously and their care is performed exclusively by the male (Bruning 1974, Fernández and Reboreda 1998). After the females complete the laying for the first male they can copulate and lay eggs for another male (Muñiz 1885, Bruning 1974).

Here, we evaluated the extent of Greater Rhea male parental care during egg and chick stages. We measured nest attention by the male and its effect on the viability and survival of eggs. We tested whether male absences during the incubation were timed to avoid embryos reaching lethal temperatures during development, or to reduce the risk of egg predation. We evaluated the effect of nest attention on the viability of the eggs by comparing temperature of eggs during the day in nests with and without male attention. Similarly, we evaluated effect of male care on the probability of egg predation by comparing the survival of eggs in nests with and without male care. In addition, we assessed the extent of parental care after hatching and evaluated its relative cost by comparing the time allocated to feeding and vigilance by males with chicks, nonreproductive solitary males and males in nonreproductive groups.

Methods

Study area.—The study was conducted during the breeding (August–January) and nonbreeding (January–July) seasons of 1993–1997, in two spatially contiguous cattle ranches of 3,500 and 800 ha. Those ranches were located near the town of General Lavalle in the province of Buenos Aires, Argentina (36°25′S, 56°56′W). A population of ~400 rheas is maintained on that study area, with a sex ratio biased slightly towards males (55% males and 45% females). The study area is a temperate grassland included in the so-called flooding pampa (Soriano 1991). The area is flat, low, and marshy, with little of the land rising >10 m above sea level. Native vegetation is composed of short grass species with scattered patches of woodland in the higher areas. That area is used almost exclusively for cattle husbandry and still has a few wild populations of Greater Rheas. In our study site, adult rheas do not have natural predators at present (i.e. cougars [*Felis concolor*]) but Crested Caracara (*Polyborus plancus*), Chimango Caracara (*Milvago chimango*), gray foxes (*Dusicyon gymnocercus*), grisons (*Galictis* sp.), and opossums (*Didelphis albiventris*) prey heavily on rhea chicks. Other non-native predators that could attack both adults and chicks are feral dogs (M. Beade pers. obs.) but we have no evidence that that type of predation had occurred during the study period.

Nest searching.—During each breeding season we searched for nests intensively all over the study site. We found 105 active nests, mainly while driving slowly across the landscape. We followed the fate of each nest until the eggs hatched or the nest failed. Nests were visited between 0900 and 1700 hours and the visits lasted <20 min. Normally, the male resumed incubation between 5 and 30 min after we left the nest. Visits were kept as brief and infrequent as possible to minimize the risk of investigator-induced desertion. We have no evidence that our disturbance could have affected nesting success. We dated the start of laying either directly (we knew the date of laying of the first egg) or indirectly by backdating. In those last cases the start of laying was estimated as the date of hatching minus 40 days or by the color of the eggs (they are light yellow when laid but become white in approximately five days). The length of the nesting period was estimated from 22 nests that were found at an early stage of the egg-laying period (they had between one and five eggs) and that hatched chicks. We consider the nesting period as the time elapsed from the day the first egg was laid until the day the male left the nest with the chicks.

Incubation behavior.—We estimated the proportion of time that a male incubated eggs through (1) focal observations of nests, and (2) by measuring the variation of egg temperature using miniature temperature loggers. We conducted focal observations on 18 nests that were in laying (days 1–10 since the laying of the first egg), three in early incubation (days 11–20), eight in midincubation (days 21–30), and 10 in late incubation (days 31–40). All observations were conducted in different nests except for one nest that was observed during mid- and late incubation. Observations were conducted from a vehicle >200 m away from the nest, between 1000 and 1700 hours. Length of the focal observations varied from 30 min to 7 h, and the total time of observation was 31.5 h. Because our observations varied in length and there were cases in which the male was at the nest all the time, to estimate the percentage of nest attention we pooled the focal observations of nests that were at the same stage of incubation.

Additionally, in 11 other nests we registered egg temperature using a miniature temperature logger (Tinytalk-temp, Orion Components, Sussex, United Kingdom). The thermistor of the temperature logger was introduced in a fresh natural orphan egg (unattended eggs laid far from active nests; Navarro et al. 1998) through a small hole in the equatorial plane and fixed to the eggshell with epoxy adhesive. The egg was attached to the center of the nest and the data logger was hidden under the nest. The data logger automatically recorded the temperature at 3.8 or 6 min intervals during four or six days, respectively. We monitored egg temperatures in those 11 nests totaling 40 nest-days. Because males are more likely to desert the nest when disturbed at an early stage of the nesting cycle (Fernández and Reboreda 2000), we monitored the majority of the nests (9 of the 11 cases totaling 34 nest-days) during mid- or late incubation. In the other two cases we started the monitoring of the nest three and five days after the laying of the first egg. None of the nests used for monitoring male activity was deserted. We used the decrease in egg temperature to determine when the male left the nest (Hainsworth et al. 1998, Flint and Grand 1999). We previously estimated egg cooling-rate of Greater Rhea eggs by heating six fresh eggs up to 33°C and then placing them in an environment at a temperature of 25°C, similar to temperatures registered in our study area between 1100 and 1300 hours (the warmest time of the day). We estimated egg cooling-rate by dividing the initial difference in temperature between eggs and the environment by the time elapsed until eggs reached a thermal equilibrium with the environment. The estimated egg cooling-rate for a temperature gradient of 8°C was $0.063 \pm 0.01°\text{C min}^{-1}$. We assumed that the male left the nest when the difference in egg temperature was $|T_{(t)} - T_{(t-1)}| > 1°\text{C}$, where $T_{(t)}$ and $T_{(t-1)}$ are egg temperatures at a time interval of 15 min when data loggers were set at 3.8 min intervals or 18 min when they were set at 6 min intervals. We considered that the male was outside the nest since the time at which the difference between $T_{(t)}$ and $T_{(t-1)}$ was negative until the time it was positive (i.e. the male resumed incubation). Although the sun can heat eggs when the male is absent (particularly at midday), unattended eggs never reached temperatures >30°C (see below). Therefore, it was possible for us to discriminate between an increase in temperature produced by the Sun and one produced by males when they resume incubation.

We also measured variation in egg temperature in three experimental nests (nests without male attention). We used nests that had been previously deserted as experimental nests. In each nest (clutch sizes of 16, 21, and 23 eggs) we fixed one egg with a thermistor inside, to the center of the nest in a similar way that we did for the active nests (see above).

We obtained hourly records of the environmental temperature during the days when we collected data with the temperature loggers. Temperature records were collected by Prefectura Naval Argentina at the town of General Lavalle, <20 km away from our study site.

Estimation of energy transfer to eggs.—The energy that incubating males transfer to eggs was estimated using the Kendeigh equation (Kendeigh 1963), which calculates the energy needed to keep the temperature of the eggs within the normal range of incubation. That equation has the form:

$$\text{kcals} \times \text{day}^{-1} = n \times w \times h \times b \times (t_e - t_{na}) \times (1 - c \times a) \times i \,/\, 1{,}000$$

where n is the number of eggs in the nest, w is the average weight of the egg (grams), h is the specific heat of the egg (cal g^{-1} °C^{-1}), b is the cooling rate of the egg (°C h^{-1} Δt^{-1}), t_e is the egg temperature (°C), t_{na} is the nest air temperature (°C), c is the proportion of the surface of the egg covered by the incubating bird, a is the proportion of time that the bird remain at the nest, and i is the time interval in hours (24 h if energetic cost is estimated for a day, i.e. kilocalories per day).

For that calculation we assumed that the weight of an egg was 647 g and the number of eggs in the nest were 25 (Fernández 1998). We also assumed that the proportion of the surface of the egg covered by the bird during incubation was 0.7. Because the proportion of time that the bird remains at the nest during incubation varies with the time of the day (see below), we used an hourly based estimation (from our data) of the proportion of time that the bird was at the nest. We assumed that the specific heat of the egg was 0.78 cal × g^{-1} × °C^{-1}, as that value is considered reasonable for most precocial species (Ricklefs 1974). The cooling rate of the eggs was $0.48°C_{egg} \times °C_{air}^{-1} \times h^{-1}$. Because nest air temperature (t_{na}) varied with time of day and breeding season, to estimate the energy transferred to eggs we took hourly values of nest air temperature during 40 consecutive days from a database with temperature records collected during the 1993–1995 breeding seasons. We used those values to perform 82 estimations of the energy transferred to eggs during incubation.

Effect of nest attention on egg survival.—We evaluated the effect of nest attention on the probability of egg survival by comparing the rate of egg losses in active nests and in nests not attended by the male (experimental nests). We used 30 nests that had been deserted at different stages of the nesting period as experimental nests. Those nests did not differ in concealment from active nests (Fernández and Reboreda 2002). We collected all the eggs from the deserted nests and after 7–10 days we added between 7 and 30 fresh eggs to each nest. We measured the losses of eggs during the following 30 days by checking the nest at one to five day intervals. Although some eggs in experimental nests could begin to rot and therefore attract predators to the nest as a result of the long exposure, natural nests very often also have rotten eggs (mainly at advanced stages of incubation). Therefore, we assumed that the main difference between experimental and natural nests was male attention. To calculate the daily rate of egg losses we used the Mayfield method (1975). Because that method uses only information from the period during which the nest is under observation, it avoids the bias introduced by differences in the time of exposure. The daily rate of egg losses was estimated by dividing the number of eggs lost by the number of days that each nest was under observation. We evaluated the effect of number of eggs in the nest on daily rates of egg losses by a regression analysis, with number of eggs in the nest as independent variable and daily rates of egg losses as dependent variable. Daily rates of egg losses were square root transformed to meet assumptions of normality.

Parental care and survival of the chicks.—We evaluated the relative cost of parental care of the chicks by comparing the proportion of time allocated to vigilance and feeding by males with chicks, solitary males, and nonreproductive males in groups of adults. We conducted focal observations with 12 × 50 binoculars from inside a vehicle at distances from 100 to 300 m. We started recording of the data 15 min after arriving at the place where the birds were foraging. They became accustomed to the presence of the vehicle within the first 5 min. Data were collected from 0730 to 1930 hours and observations were audio or video recorded and later analyzed with a computer running an event recorder program (ETHOLOG 2.0). We measured proportion of time that males allocated to the following behaviors (Reboreda and Fernández 1997): vigilance, feeding, walking, preening, resting, and aggressive interactions. We considered that a bird was vigilant when it stood with its head up, and that it was feeding when it had the head down and was pecking among the vegetation. Because rheas walk almost continuously while foraging, we considered that they were walking instead of foraging only when the head was above the body while walking. A record of a focal animal ended after 10 min of observation or when the animal moved out of sight. We excluded from the analysis records that lasted <3 min.

We collected data from 30 males with chicks, 15 solitary males and 85 males in nonreproductive groups. Data were collected from late October to early July. No site was used more than once for observations, but because birds were not marked and moved freely within the study area, repeated observations of the same bird cannot be excluded. However, if we observed a bird more than once, it was on a different date and at a different place. Rheas were considered to be solitary when no other rheas were within a radius of 100 m, whereas they were considered to be part of a group if they were within 50 m from one another. We adopted that criterion because in all cases the distance to the nearest neighbor was either <50 m (normally 10–30 m) or >100 m. Males in groups of different size (from two to nine individuals) were pooled for the analysis because in a previous study we did not detect differences in individual vigilance between males foraging in groups of those sizes (G. J. Fernández and J. C. Reboreda unpubl. data).

During the 1994–1995 nonbreeding seasons, we evaluated the extent of posthatching parental care and rate of chick survival through regular census at the study area. During each census, we determined the number of groups of males with chicks, the location of each group, and the number of chicks within each group. The groups of males with chicks were identifiable by their size and because males remained close to the place where they nested for at least one month after hatching.

Results are presented as mean ±SE otherwise stated. All significance levels are for two-tailed tests.

RESULTS

Incubation behavior.—We estimated the length of the nesting period from a sample of 22 nests (clutch size = 25 ± 2, range: 12–56 eggs) as 42 ± 3 days (mean ±SD; range: 38–50 days) and it was positively associated with clutch size (F = 16.1, df = 1 and 20, $P < 0.001$, $r^2 = 0.45$). Visits to nests and focal observations showed that males started to care for the eggs when there were as few as two eggs. The proportion of time that males spent at the nest increased as the nesting period progressed, with males spending more time during mid and late incubation (days 20–40) than earlier (homogeneity G-test, G = 18.8, df = 3, $P < 0.001$; Fig. 1). Records of egg temperatures during mid and late incubation (n = nine nests, clutch size = 22.4 ± 2.8, range: 15–44 eggs) showed that during those stages males spent 97.5 ± 0.4% of the time at the nest and that the frequency of pauses during the incubation was 1.7 ± 0.4 day^{-1}. The proportion of time that the males were absent from the nest varied with the time of the day (Friedman ANOVA, $\chi^2 = 82.8$, df = 23, $P < 0.001$, $n = 10$). Approximately 64% of the absences during mid and late incubation occurred between 1100 and 1700 hours, at the warmest time of the day (Fig. 2). Proportion of time outside the nest was <2% when the temperature of the environment <19°C, but increased up to ~10% when the temperature rose from 19 to 22°C (polynomial regression analysis on arcsine-squared root transformed proportion of time at the nest, F = 49.3, df = 2 and 21, $P < 0.0001$, $r^2 = 0.81$). Nest absences lasted on average 20.5 ± 2.8 min (range: 3–87 min) and there was no effect of environment temperature on the length of the pause (regression analysis, F = 0.19, df = 1 and 62, $P = 0.67$). Time out of the nest was spent in foraging nearby (<50 m from the nest). We also observed that during incubation, the male stood over the eggs briefly (<1 min h^{-1}) while he rotated the eggs.

Effective incubation of eggs appeared to start five to seven days after the laying of the first egg. At that time we detected an increase in nest attendance by the male and egg temperature became constant (Fig. 3A). After incubation started, mean egg temperature at the center of the

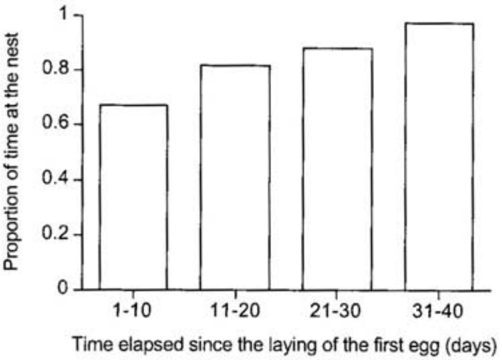

FIG. 1. Bars show the proportion of time that males were present at the nest at different stages of the nesting cycle. Laying (days 1–10), early incubation (days 11–20), midincubation (days 21–30), and late incubation (days 31–40). Data correspond to focal observation of 18 nests that were in laying, 3 in early incubation, 8 in midincubation and 10 in late incubation.

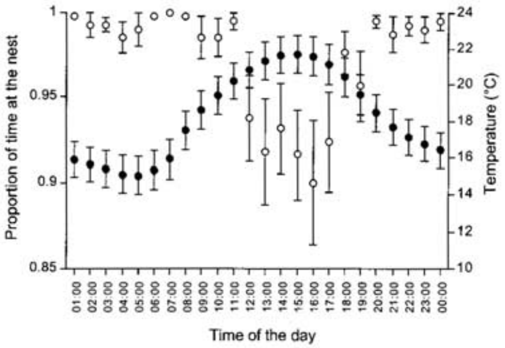

FIG. 2. Open circles show the proportion of time (±SE) that males remained at the nest during mid and late incubation as a function of the time of the day. Filled circles present average air temperature profile (±SE) over the same period that observations were made at the nests. Data were collected by measuring variation of egg temperature through a miniature temperature logger introduced in the egg (see text for details).

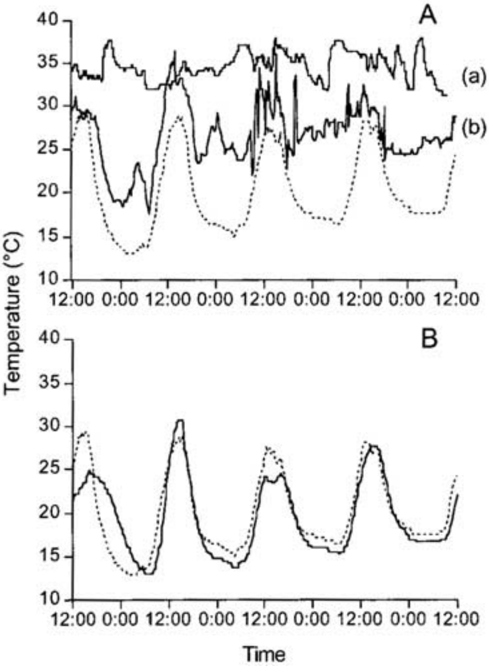

FIG. 3. Temperature records for nests at different stages of incubation. (A) Solid lines show egg temperature in (a) a nest at an advanced stage of the incubation (from day 25 to 29), and (b) a nest during egg laying (from day 3 to 7). Broken line is a record of air temperature. (B) Temperature of eggs (solid line) and air (broken line) in an unattended nest.

nest was 33.9 ± 1.7°C (range: 31.5–36.2°C, $n = 9$ nests; Fig. 3A). Variability in egg temperature was high at the start of laying, decreased as laying progressed, and remained low at advanced stages of incubation. Temperature of eggs did not differ between day and night (paired *t*-test, $t = 0.07$, df = 8, $P = 0.94$) and never fell below 27°C or exceeded 40°C.

Egg temperatures in nests that were not attended by the male were closely associated to the environment temperature ($r^2 = 0.89$, $n = 725$, $Z = 38.04$, $P < 0.001$; Fig. 3B). During the warmest time of the day, temperature of eggs in unattended nests reached values of 30–35°C and during the night fell below 15°C.

Energetic cost of the incubation.—Estimated energy transferred to eggs during incubation varied from 47,033 to 65,130 kcal (mean = 53,202.4 ± 5,916.9 kcal). Those values are equivalent to 5 kg of lipids and represent approximately 15–20% of the weight of an adult male (~30 kg; Sick 1985).

Effect of nest attention on egg survival.—Rate of egg loss was higher in unattended than in attended nests (0.08 ± 0.17 vs. 0.014 ± 0.003 eggs × nest day^{-1}; Mann-Whitney test, $Z = 3.62$, $n_1 = 30$ nests, $n_2 = 64$ nests, $P < 0.001$). We did not detect an effect of the number of eggs in the nest on the rate of egg losses in either unattended or attended nests (regression analysis on square root transformed values, $F = 0.88$, df = 1 and 28, $P = 0.35$ for unattended nests, and $F = 0.04$, df = 1 and 28, $P = 0.83$ for attended nests).

Parental care and survival of the chicks.—Males took care of the chicks for approximately four to six months. We observed a male caring for the chicks in five of six groups of four month old chicks and in two of four groups of six month old chicks but we did not observe any adult male in eight groups of seven month old chicks. Males with chicks spent less time in feeding and more time in vigilance than solitary males or males in groups of adults (Kruskall-Wallis tests, $H = 38.4$, df = 2, $P < 0.001$ for feeding and $H = 45.4$, df = 2, $P < 0.001$ for vigilance and contrasts *a posteriori*, $P < 0.05$; Fig. 4). To evaluate if there was an effect of the age of the chicks on the extent of parental care provided by the male, we compared time spent in vigilance and feeding by males with chicks of different ages (up to 30 days old, 30–60 days old, 60–120 days old, and 120–180 days old). Percentage of time allocated to feeding increased with age from 30–60 days old chicks up to 120–180 days old chicks, but males with chicks up to 30 days old spent more time feeding than males with chicks 30–60 days old (Kruskall-Wallis test, $H = 9.93$, df = 3, $P < 0.05$ and contrasts *a posteriori*, $P < 0.05$; Fig. 5). Similarly, percentage of time allocated to vigilance differed between 30–60 and 120–180 days old chicks (Kruskall-Wallis test, $H = 9.02$, df = 3, $P < 0.05$ and contrasts *a posteriori*, $P < 0.05$; Fig. 5).

In some cases ($n = 6$ groups), we observed a male with a large group of differently aged chicks. Those groups were the result of the fusion of different groups of chicks (Codenotti and Alvarez 1998, Labaqué et al. 1999) and could imply an additional parental cost if the proportion of time spent in vigilance increased with the number of chicks. We did not detect an association between proportion of time that a male allocated to vigilance and number of chicks of its group (Spearman rank correlation, $n = 23$ groups, $\rho = 0.03$, $Z = 0.14$, $P = 0.89$). For

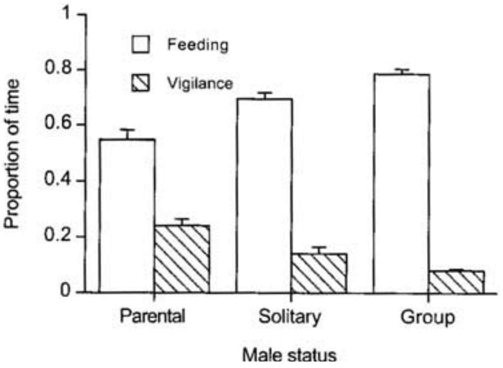

FIG. 4. Proportion of time (±SE) allocated to feeding and vigilance by males with chicks (n = 30), solitary males (n = 15) and males in nonreproductive groups (n = 85).

that analysis, we used groups of males with chicks up to 120 days old because we did not detect an effect of age of chick within that range in the proportion of time that males allocated to vigilance (Kruskall-Wallis test, $H = 1.4$, df = 2, $P = 0.49$).

Mortality declined as chicks aged. Approximately 60% of the chicks reached 40–50 days of age whereas 40–50% of chicks reached the age of one year. To analyze if there was any temporal effect on chick survival we compared proportion of chicks that survive until four months of age for early and late breeders. There was no difference in survival rate until the first four months of age between chicks that hatched in the first (October–November) and in the second (December–January) half of the breeding season (slope t-test on ln-transformed data, $t_{(45)} = 0.02$, $P > 0.05$). Similarly, there were no significant differences in average number of chicks hatched per nest during the first and the second half of the breeding season (13.3 ± 2.3, n = 6 nests vs. 14.6 ± 1.2, n = 20 nests, ANOVA, $F = 0.26$, df = 1 and 24, $P = 0.61$).

DISCUSSION

Incubation behavior.—Greater Rhea males remain at the nest approximately 65–70% of the time during egg laying and that percentage increased up to 97% as incubation proceeded. The lower proportion of time at the nest during egg laying could be the result of the need of the male to copulate regularly with females of his harem and to guard them from other males (G. J. Fernández pers. obs.). Females rheas lay eggs every 2–3 days for up to 15 days (Fernández and Reboreda 1998) and number of eggs in the nest increases in a negatively accelerated way (the percentages of eggs laid at days 5 and 10 and 15 are 58, 89 and 96, respectively; Fernández and Reboreda 1998). Therefore, as laying proceeds, the cost of cuckoldry for the incubating male would decrease in a negatively accelerated manner. In addition, because embryos at an early stage of development have a greater tolerance to fluctuations in temperature (Webb 1987), cost of the interruptions in incubation—in terms of hatchability of the eggs—would be lower during the egg-laying stage than later.

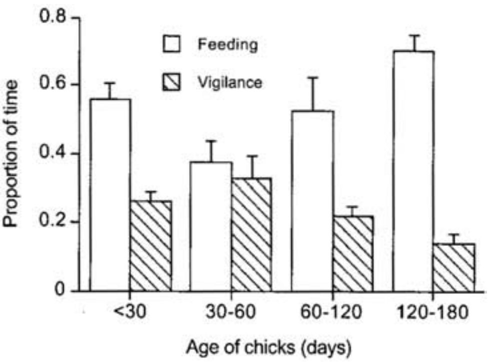

FIG. 5. Proportion of time (±SE) allocated to feeding and vigilance by males with chicks of up to 30 days old (n = 12), from 30 to 60 days old (n = 7), from 60 to 120 days old (n = 4), and from 120 to 180 days old (n = 7).

The high percentage of time that males spend at the nest during incubation may enhance viability of the embryos by preventing them from reaching lethal temperatures (egg viability hypothesis; Arnold et al. 1987). The critical values of temperature at which there is no viable embryonic development are <27°C (Carey 1980, Hafton 1988) and >40°C (Bennett and Dawson 1979, Dawson 1984, Williams and Ricklefs 1984). The majority of male absences were at the warmest hours of the day (1100–1700 hours) and those absences were relatively brief, usually lasting <30 min. It is very unlikely that eggs reached temperatures that affected their viability during those absences because at that time of the day, egg temperatures in unattended nests were >27°C and <35°C. On the contrary, egg temperatures in unattended nests decreased to values <27°C during the night and, therefore, at that time males enhanced viability of the embryos by keeping their temperatures above lethal minimum. The effect of male care during the day would be less important for keeping embryos below lethal temperatures, but still it could improve viability of the eggs by avoiding high rates of water loss. In contrast, in Ostriches (*Struthio camelus*), egg temperature in unattended nests reached lethal levels during both day and night (Bertram and Burger 1981, Bertram 1992). Our study was carried out in a temperate region and therefore daylight temperatures during the breeding season were not as high as the ones experienced by Ostriches. However, for rheas living in subtropical areas, nest attention could also avoid egg temperatures increasing up to lethal level for embryos.

In addition to providing a favorable thermal environment for embryo development, the high percentage of time that males spent at the nest enhanced the survival of eggs by reducing the risk of predation. The higher survival of eggs in attended nests resulted presumably from either a decrease in the visibility of nests or by expelling potential predators. We observed several instances of Crested and Chimango caracaras feeding on rhea eggs in deserted nests. Gray foxes are also known to prey on rhea eggs (R. Paso pers. comm.). It seems unlikely that presence of a Greater Rhea male might reduce detectability of the nest, especially in the case of aerial predators, but it can easily deter those predators and therefore reduce probability of egg losses.

Parental care of the chicks.—Parental care after hatching involved an important investment of time. Males spent >20% of the daylight time in vigilance until chicks were four months old. That percentage was ~3× the amount of time spent by males in nonreproductive groups, and 2× as much as time spent by solitary males, indicating that the higher level of vigilance by males with chicks was not simply the result of a group size effect (i.e. solitary males spend more time in vigilance than males in groups; Reboreda and Fernández 1997). Proportion of time allocated to vigilance decreased and proportion of time allocated to feeding increased as the chicks grew. However, males with chicks up to 30 days old allocated more time to feeding than males with older chicks. We presume that that was a consequence of the male's need to recover energy after the long fasting period during incubation. The high level of parental vigilance at that stage may be critical for the survival of the chicks, particularly in open areas, as was the case in our study. On four occasions we observed Crested and Chimango caracaras catching one month old chicks. Also, foxes and ferrets were common terrestrial predators in our study area. Chick mortality was high during the first months after hatching and only 60% of chicks reached 40–50 days of age. Mortality rate declined as chicks grew and approximately 40–50% of chicks survived until one year of age. In association with the decrease in chick mortality, percentage of time allocated to vigilance by males with chicks also decreased with chicks' age. That reduction could reflect either a decrease in chick vulnerability or the male's need to build their reserves for future breeding attempts.

Like other studies of rheas (Codenotti and Alvarez 1998, Lábaque et al. 1999) we also observed that the male incorporated to its group chicks from other groups. That "chick adoption" behavior has also been described for Ostriches, where large crèches of differently aged chicks are cared for by only two adults (Sauer and Sauer 1966). There was no apparent cost (i.e. a decrease in proportion of time allocated to foraging) for adopting chicks from other groups. Because the small number of groups of males with adopted chicks, we were unable to test if that behavior resulted in a benefit for the adopting male through a reduction of the risk of predation of its own chicks by dilution with nonkin chicks.

Energetic cost of parental care.—Males transferred as estimated 53,000 kcal to eggs during incubation, the equivalent of 5 kg of lipids (approximately 18–20% of its body weight). Those values are probably a slight overestimate of the energy necessary for incubation because we assumed that incubation starts at day one and all eggs are laid at the same time and are equally covered by the male (the latter assumption is clearly violated in large clutches). Because rhea males rarely leave the nest to feed, our estimate provides an approximation of the net energetic cost of incubation. The estimated energetic cost for rheas is similar to that measured in Emus (*Dromaius novaehollandiae*), another ratite species in which the male performs all incubation. Male Emus lost 7 kg (about 17–20% of their body weight) during 56 days of incubation (Dawson et al. 1984). Similarly, Brown Kiwi

(*Apteryx australis*) males lost ~23% of their body weight during 91 days of incubation, although in that species incubation is partially shared with females (Taborsky and Brugger 1994). The energetic investment in parental care after hatching is more difficult to estimate. However, the lower percentage of time allocated to feeding by males with chicks provides a relative estimation of the cost of chick care. Because the care of chicks lasts until they are 4–6 months old, that cost would be more important than previously supposed.

Cost of parental care and the evolution of rhea mating system.—Our results indicate that Greater Rhea males require high levels of energetic reserves to start a breeding attempt. That energetic demand could explain why <20% of the males attempt to nest during the breeding season (Fernández and Reboreda 1998) and might also be responsible for the high rate of early nest desertion that we observed (Fernández and Reboreda 2000). The high energy requirement might also affect the extent of polyandry because a low proportion of males in adequate physical condition may result in a female-biased operational sex ratio, which will favor polygyny. Differences in male condition could also favor polygyny if females prefer to mate with males with adequate fat reserves, as happens in other precocial species in which males incubate (Petrie 1983). An alternative explanation for the extent of polyandry and polygyny in Greater Rheas is that the cost of egg production constrains the number of females that can lay eggs. King (1973) estimated that for galliforms, daily maximum cost of egg production is 21–30% of daily energy intake. Although relative egg size in ratites (except for kiwis) is lower than in other groups (Clutton-Brock 1991), egg laying would require the investment of ~50% of the energy invested by the male during incubation but in a shorter period (approximately 10–15 days). If females were limited in the number of eggs they can lay, they should select high quality males and, therefore, not all males would have the opportunity for mating.

Ligon (1993, 1999) has proposed that the initial form of parental care in birds was protection of eggs from predators. According to that author, the cost of nest defense for females (a reduction in the production of eggs) would be higher than the cost of opportunity for males (additional matings). Therefore, females should not provide further parental care after laying and should produce additional eggs, whereas males should assume the parental duties. Thus, uniparental male care might have evolved as a result of the necessity of early nest attendance critical for egg or nest survival.

Our rhea data, as well as that of Ostriches, are consistent with that hypothesis. Ostriches have high rates of egg and nest predation during laying (Bertram 1992), and eggs in unattended nests can reach lethal temperatures (Bertram and Burger 1981). High egg temperatures in unattended nests might also be critical for other ratites, like Emus, which have dark eggs (contrary to rheas and Ostriches which have white eggs).

With males assuming care of eggs and chicks, females were freed of parental duties, which may have favored the evolution of polyandry. In addition, the high energetic requirement of incubation would presumably permit reproduction only in males in high physical condition. On the other hand, polygyny could have evolved as a result of the selective pressure for reducing the costs of males adopting uniparental care. The outcome of that scenario is a female-biased operational sex ratio that might favor a polygynous mating system with communal egg laying (Vehrencamp 2000), as happens in rheas and Ostriches, and strong female–female competition, like the one observed in Emus (Coddington and Cockburn 1995).

In summary, in rheas as well and in other ratites, the high energetic costs associated with incubation and post-hatching parental care would favor paternal care and a mating system that combines polyandry and polygyny. Further data of the energetic cost of breeding for males and females of other ratite species would be valuable for testing that hypothesis.

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